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FLOWER BIOLOGY OF SIX CULTIVARS OF THE BROMELIACEAE I. POLLEN, PISTIL, AND PETAL APPENDAGES

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ABSTRACT. The authors determined morphometric data of different floral features and in vitro pollen germination of six cultivars representing four genera and two subfamilies of Bromeliaceae. Important floral characteristics for plant breeding are pollen germination and style length. Pollen viability was for all cultivars more than 40% and high enough for successful pollination. Stylar length varied much for the different cultivars. Scanning electron microscopy (SEM) was used to examine important flower characteristics. The pollen of *Aechmea fasciata* were biporate, and those of *Tillandsia cyanea*, *Vriesea* × *viminalis* × *carinata* and *V. splendens* were monosulcate. Pollen grains of *A. chantinii* and *Guzmania lingulata* were inaperturate. The exine layers of all taxa were reticulate in structure with the exception of *A. chantinii*, which was smooth. Four stigma types were detected: convolute-blade, conduplicate-spiral, simple-erect, and coralliform. Petal appendages of *Vriesea* were tongue-like and absent in *G. lingulata* and *T. cyanea*. *Aechmea fasciata* and *A. chantinii* had complex petal appendages. Ovules of all cultivars possessed characteristic chalazal appendages.

Key words: Bromeliaceae, ovary, ovules, petal appendages, pollen, stigma

INTRODUCTION

Bromeliaceae are predominantly neotropical epiphytic herbs or terrestrial xerophytes comprising about 62 genera and 2800 species (Smith & Downs 1974, Benzing 1980, W. Till unpubl. data). Bromeliads tend to be ornamental and are easy to cultivate. In spite of the size of the family and its horticultural importance, little is known about the floral architecture and reproductive biology (Gilmartin & Brown 1986, Benzing 2000). The family is traditionally divided into three subfamilies: Pitcairnioideae, Tillandsioideae, and Bromelioideae (Smith & Downs 1974, 1977, 1979). Pitcairnioideae and Tillandsioideae have mostly hypogenous flowers, and the fruits are capsules. Bromelioideae have epigenous flowers and baccate fruits (Benzing 1980, Dahlgren et al. 1985). The flower structure of bromeliads is neither primitive nor highly evolved. The flowers are mostly bisexual and basically three-parted; there is a three-chambered ovary topped by a style with a three-lobed stigma. Three petals alternate with an equal number of smaller sepals. The six stamens (usually) are positioned in two whorls of three each (Benzing 1980, 2000). Bromeliads, like most monocots have a hollow (open) style. The ovules are anatropous, bitegmic, and crassinucellate with the micropyle formed by the inner integument (Davis 1966, Johri et al. 1992). Bromeliads have wet stigmas with a low to me-

dium amount of specialized glandular cells, the papillae (Heslop-Harrison & Shivanna 1977, Knox et al. 1986).

Brown and Gilmartin (1989) studied more than 400 Bromeliaceae for stigma morphology. Five types account for all known variation. Small paired or single outgrowths from the base of each petal, known as petal appendages are common in Bromeliaceae and are most probably involved in intrafloral nectar management (e.g., nectar retention, presentation, and delivery) (Brown & Terry 1992). An important taxonomic aspect is pollen grain appearance (Halbritter 1992). The most significant diagnostic features of pollen grains are their size, shape, apertures (germination pores), and exine surface structure (Shivanna & Rangaswamy 1992). Pollen viability indicates the ability of the pollen grain to deliver sperm cells to the embryo sac following compatible pollination (Shivanna et al. 1991, 1997). Tests for germination capacity and normal pollen tube growth on in vitro media provide a direct and reliable assessment of viability (Heslop-Harrison et al. 1984). Pollen of many plant species, typically binucleate pollen, germinates and grows well in culture. Bromeliaceae have binucleate pollen (Brewbaker 1967, Johri et al. 1992).

The goal of this study was to present a survey on flower characteristics: morphometric data, stigma type, papillae, petal appendages, pollen grain, and ovule morphology of six economically and horticulturally important cultivars. Most studies on bromeliad flower morphology deal

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TABLE 1. Flower characteristics at anthesis of *Aechmea fasciata* (AF), *Aechmea chantinii* (AC), *Vriesea* × *viminialis-rex* × *carinata* (VMC), *Vriesea splendens* (VS), *Guzmania lingulata* (GL), and *Tillandsia cyanea* (TC).

Plant	AF	AC	VMC	VS	GL	TC
Length (cm)						
Bract	6.1 ± 0.6	0.9 ± 0.1	4.0 ± 0.3	6.3 ± 0.2	—	5.1 ± 0.3
Sepal	2.5 ± 0.1	1.7 ± 0.1	3.0 ± 0.2	2.4 ± 0.2	2.4 ± 0.2	4.2 ± 0.2
Petal	4.7 ± 0.2	2.3 ± 0.1	4.7 ± 0.2	6.6 ± 0.2	5.1 ± 0.2	7.9 ± 0.4
Stamen	3.4 ± 0.2	1.5 ± 0.1	4.3 ± 0.3	6.1 ± 0.6	4.5 ± 0.3	2.7 ± 0.3
Anther	0.6 ± 0.0	0.3 ± 0.1	0.7 ± 0.1	0.5 ± 0.0	0.6 ± 0.1	0.7 ± 0.1
Stigma	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.3 ± 0.1
Style	3.2 ± 0.2	1.5 ± 0.1	4.8 ± 0.2	5.7 ± 0.2	4.1 ± 0.2	0.6 ± 0.1
Pistil	4.3 ± 0.2	2.3 ± 0.1	6.1 ± 0.2	6.9 ± 0.3	5.2 ± 0.3	1.8 ± 0.1
Width ovary (cm)	0.9 ± 0.1	0.8 ± 0.1	0.7 ± 0.0	0.6 ± 0.1	0.3 ± 0.0	0.3 ± 0.0
% Pollen germination	84 ± 15	63 ± 19	57 ± 21	46 ± 21	46 ± 21	56 ± 16
Length (μm)						
Pollen tube	1789 ± 809	2791 ± 562	1068 ± 226	1145 ± 283	2029 ± 212	1445 ± 461
Pollen	74 ± 5	62 ± 3	78 ± 20	61 ± 3	64 ± 6	59 ± 4
Width pollen (μm)	47 ± 2	62 ± 3	49 ± 12	41 ± 2	64 ± 6	34 ± 2
No. ovules	304 ± 38	90 ± 32	442 ± 100	443 ± 33	448 ± 83	391 ± 83
Length ovule (μm)	246 ± 35	206 ± 7	189 ± 13	201 ± 9	240 ± 13	270 ± 28
Width ovule (μm)	169 ± 25	160 ± 11	96 ± 6	112 ± 6	103 ± 5	131 ± 12

with field collected specimens or species from botanical gardens. Less is known about commercial cultivars, however such information is of interest for plant breeding. Existing studies mostly focus on one aspect of flower morphology such as pollen, petal appendages, or stigma structure. This study is unique in that it combines all these data and highlights the information of interest for plant breeding.

MATERIAL AND METHODS

Cultivars *Aechmea fasciata* and *A. chantinii* (Bromelioideae) and *Vriesea* × *viminialis-rex* × *carinata*, *V. splendens*, *Guzmania lingulata* var. *minor*, and *Tillandsia cyanea* (Tillandsioideae) were studied. *Vriesea* × *viminialis-rex* × *carinata* and *G. lingulata* var. *minor* are abbreviated as respectively *V. vr* × *carinata* and *G. lingulata*. *Aechmea fasciata* and *A. chantinii* belong to the subgenus *Platyaechmea* (Smith & Downs 1979); this subgenus has been suggested for elevation to the generic status *Hoplophytum* (W. Till unpubl. data). *Vriesea* × *viminialis-rex* was a name used to designate all branched *Vriesea* hybrids. *Vriesea carinata* and *V. splendens* belong to the subgenus *Vriesea* section *Vriesea*. *Tillandsia cyanea* is a member of the subgenus *Phytarrhiza* (Smith & Downs 1977).

Flowers at anthesis were fixed in ethanol (70%). Dehydrated flower parts were critical point dried to study surface morphology of stigma, papillae, style, petal appendage, pollen

grain, ovary, and ovules. Flower parts were examined using a JEOL JSM-5800 LV scanning electron microscope at 15 kV at Nationale Plantentuin in Meise, Belgium. Morphometric flower characteristics were determined from 20 individual flowers at anthesis from 10 different plants. *Aechmea fasciata* flowers were measured when the first flowers in the inflorescence started to bloom (1st week), at the 2nd and 3rd week, and until the end of the flowering period (4th week). Only the results of the 1st week are shown in TABLE 1. To determine pollen germination, anthers were transferred into a 1.5 ml Eppendorf tube. Pollen was isolated from the anthers by shaking them in 1 ml liquid medium (20% sucrose and 10 ppm H₃BO₃ in water). The anther-medium mix was then placed on solid medium in a petri dish (diameter 55 mm). This solid medium contained 20% sucrose, 10 ppm H₃BO₃, and 0.5% agar in water. For each germination determination, a sample of two anthers of the same flower was transferred into a petri dish; and this was repeated for 10 flowers. Petri dishes were incubated at 20°C for 24 hours in light. Pollen germination and pollen tube length were evaluated by light microscopy. Pollen grains were scored as germinated when the pollen tube length was at least twice the pollen grain length. For each flower, 200 pollen were examined for germination and 20 pollen tube lengths were measured. Light microscopy was conducted by means of an OLYMPUS BX 40. Length and width of 100 ovules and length of 100 pollen

tubes were measured using the video image analysis program Micro Image (Olympus). Fresh stigmas and petal appendages were visualized using an OLYMPUS SZX9 stereomicroscope.

RESULTS AND DISCUSSION

Flowers of *Aechmea fasciata*, *A. chantinii*, *Vriesea vr × carinata*, *V. splendens*, *Guzmania lingulata*, and *Tillandsia cyanea* were sampled indiscriminately in the inflorescence to determine the morphometric characteristics (TABLE 1). The anthers were below the stigma at anthesis (*V. vr × carinata*) or were at the same level of the stigma (other cultivars). This indicates that the flowers of these cultivars are often self-pollinated at anthesis. For crossing experiments, it is necessary to emasculate them before anthesis. Styles could be very long as in *V. splendens* (5.7 cm) or rather small as in *T. cyanea* (0.6 cm). Stylar length is important for the achievement of fertilization in cross breeding. Often the cross with the short-styled parent used as female and the long-styled parent used as male is successful, but the reciprocal is not (Liedl et al. 1996, Vervaeke et al. 2001).

In general in vitro pollen germination and pollen tube length of the studied bromeliads were high enough for pollination; this indicates that the viability was more than 40% (Knox 1984). Pollen germination achieved in vitro was comparable to that found on a compatible stigma (Vervaeke et al. 2001). Petal and pistil length and ovary width decreased progressively for *Aechmea* flowers at anthesis comparing the 1st and 4th week of blooming (results not shown). The most striking difference between 1st and 4th week of flowering was the number of ovules (304 versus 122). During the 1st week only two to five flowers bloomed each day in the inflorescence; this amount increased up to approximately 15 during the 4th week. The inflorescence of *A. fasciata* is simple but compact with few basal branches (Smith & Downs 1977). Anthesis as a rule proceeds acropetally (Benzing 2000). Flowers became smaller, however pollen germination and pollen tube length did not change. In general, examined Tillandsioideae had more ovules per ovary than did *Aechmea*.

Papillae of *Aechmea fasciata* were relatively small and few in number (FIGURE 1A). Where the stigma surface was relatively smooth, the bounding cells were referred to as "surface receptive cells" (Shivanna 1982). The papillae were free from each other and were for some of their length above the general level of the stigma surface. *Aechmea chantinii* possessed more rounded papillae (FIGURE 1B), similar to those of *Guzmania lingulata* (FIGURE 2E). *Tillandsia*

cyanea (FIGURE 2F), *Vriesea vr × carinata* (FIGURE 1C), and *V. splendens* (FIGURE 1D) had many long-drawn papillae. A transverse section of the style of *A. chantinii* revealed the hollow style canal (FIGURE 1E). Papillae of *V. vr × carinata* occurred in the transition between the stigma and style (FIGURE 1F), with the stylar canal originating from the stigma in hollow styles (Shivanna et al. 1997). The stigma of *A. fasciata*, *A. chantinii*, and *G. lingulata* exhibited only terminal papillae. *Vriesea vr × carinata*, *V. splendens*, and *Tillandsia cyanea* stigmas were completely covered by papillae.

Brown and Gilmartin (1989) examined the stigmas of more than 400 bromeliad species and identified five stigma architectures: conduplicate-spiral, simple-erect, convolute-blade, cupulate, and coralliform. According to this classification, *Aechmea fasciata* (FIGURE 2A), *A. chantinii* (FIGURE 2B), and *Vriesea splendens* (FIGURE 2D) bear a conduplicate-spiral stigma. In this organization, three flattened style branches are each folded along the axis, and the three folded branches are spiralled together. The conduplicate-spiral type is unique to Bromeliaceae and occurs nearly consistently through Bromelioideae (Brown & Gilmartin 1989). The branches of *V. splendens* were much shorter and less spiralled than those of the *Aechmea* cultivars. *Vriesea vr × carinata* (FIGURE 2C) had a convolute-blade stigma. This type consists of three laminar lobes each with a stigmatic line along at least the distal portion of the lobe (Brown & Gilmartin 1984). *Guzmania lingulata* (FIGURE 1A, 2E) possessed a simple-erect stigma, characterized by three free, erect stylar lobes, each with an introrsely oriented stigmatic line along the distal margin of the lobe (Brown & Gilmartin 1984). The coralliform stigma type, as illustrated by *T. cyanea* (FIGURE 2F), is typical for subgenus *Phytarrhiza*. It is characterized by a proliferation of irregular growth in the marginal stigmatic line of each lobe. The resulting stigmatic line bears long, densely packed papillae. Brown and Gilmartin (1989) described *T. cyanea* var. *cyanea* as conduplicate-spiral. We found no spiralled branches even before anthesis, indicating that among varieties of the same species different stigma types can occur.

Petal appendages are small paired or single outgrowths from the base of each petal (FIGURE 3). Approximately 35% of the bromeliad species are known to have petal appendages (Brown & Terry 1992). Individual appendages of *Aechmea chantinii* and *A. fasciata* were ornately fringed and tongue-like (FIGURE 3A, B). Bromelioideae had the most complex floral structure in the family and also exhibited the most complex and variable petal appendage morphology (Brown &

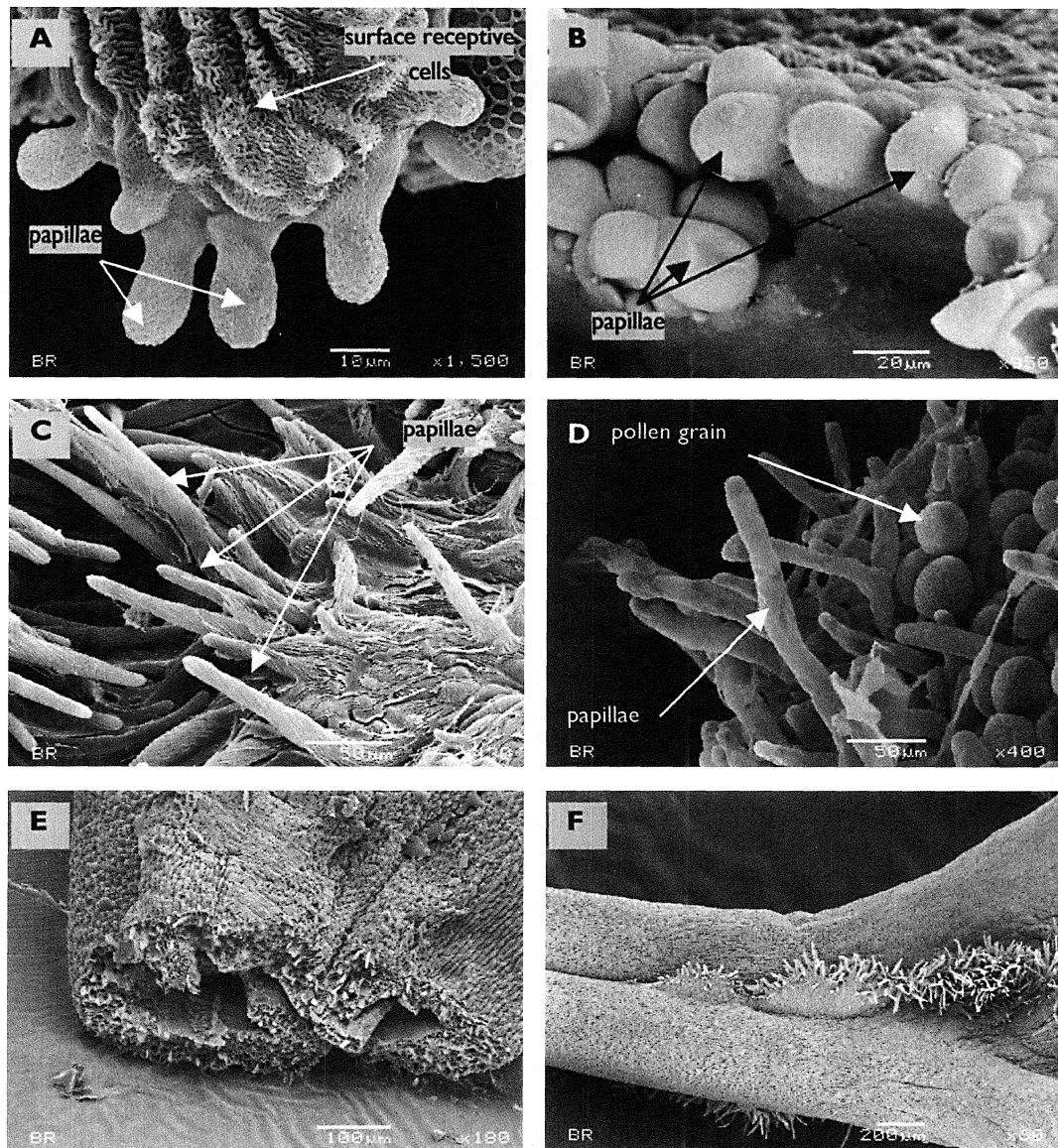


FIGURE 1. Stigma and style **A.** Papillae of *Aechmea fasciata* ($\times 1500$). **B.** Papillae of *A. chantinii* ($\times 950$). **C.** Detail of papillae of *Vriesea* \times *vimimalis rex* \times *carinata* ($\times 430$). **D.** Papillae and pollen grains of *V. splendens* ($\times 400$). **E.** Hollow style of *A. chantinii* ($\times 180$). **F.** Stigma and style of *V. vr* \times *carinata* ($\times 60$).

Terry 1992). *Vriesea vr* \times *carinata* and *V. splendens* had tongue-like blade petal appendages (FIGURE 3C, D). No appendages were found in *Tillandsia cyanea* and *Guzmania lingulata*. *Tillandsia* and *Vriesea* are separated on the basis of absence or presence of petal appendages, respectively (Benzing 1980, Brown & Terry 1992). Nevertheless, there is an overemphasis on the presence of petal appendages in the circumscription of genera in Bromeliaceae and espe-

cially Tillandsioideae. Petal appendages by themselves are not reliable generic markers. As a terminal ontogenetic character, these delicate appendages probably represent minor modifications of a more fundamental floral pattern. Features determined earlier during ontogeny should provide more superior markers for genera and taxa (Brown & Terry 1992, Benzing 2000).

Three aperture types occur in Bromeliaceae: porate (exclusively Bromelioideae), inaperturate

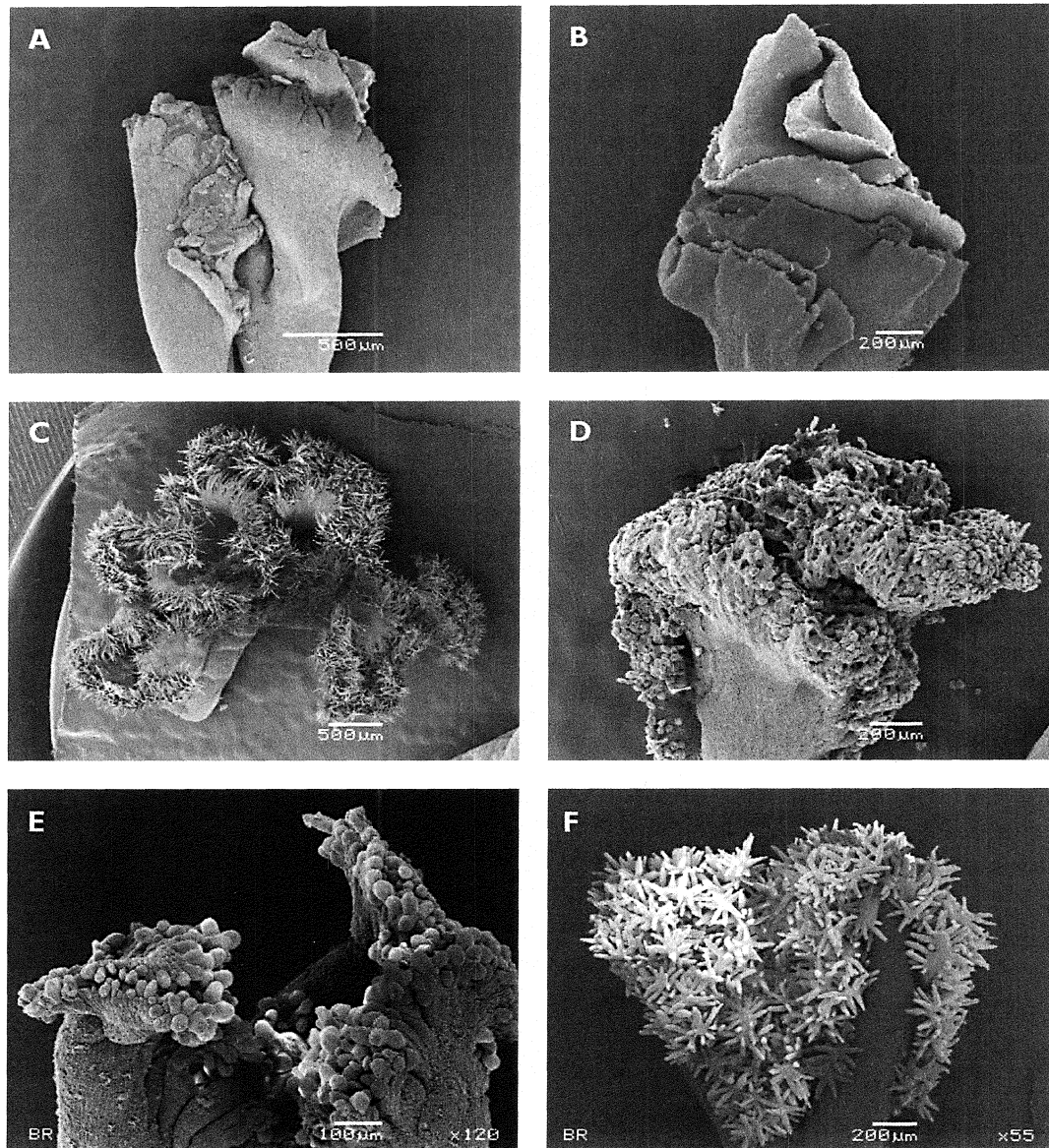


FIGURE 2. Stigma **A.** Conduplicate-spiral stigma of *Aechmea fasciata*. **B.** Conduplicate-spiral stigma of *A. chantinii*. **C.** Convolute-blade stigma of *Vriesea vr × carinata*. **D.** Conduplicate-spiral stigma of *Vriesea splendens*. **E.** Simple erect stigma of *Guzmania lingulata* ($\times 120$). **F.** Convolute-blade stigma of *Tillandsia cyanea* ($\times 55$).

(various Bromelioideae and Tillandsioideae), and sulcate (Pitcairnioideae and Tillandsioideae) (Halbritter 1992, Benzing 2000). Porate pollen grains have apertures in the exine, while pollen grains of sulcate species exhibit long furrows called sulcae (Iwanami et al. 1988). The pollen of *Aechmea fasciata* was biporate, with two germination pores or apertures opposite to each other (FIGURE 4A). *Aechmea chantinii* had spherical

pollen with a smooth exine layer without clear apertures (inaperturate) (FIGURE 4B). *Vriesea vr × carinata* (FIGURE 4C) and *V. splendens* (FIGURE 4D) were monosulcate of the “insulae” type (isolated exine elements, scattered over the sulcus area, Halbritter 1992). *Guzmania lingulata* had inaperturate pollen. Some pollen grains of *G. lingulata* were small and collapsed (FIGURE 4E). Abnormal pollen formation could be caused

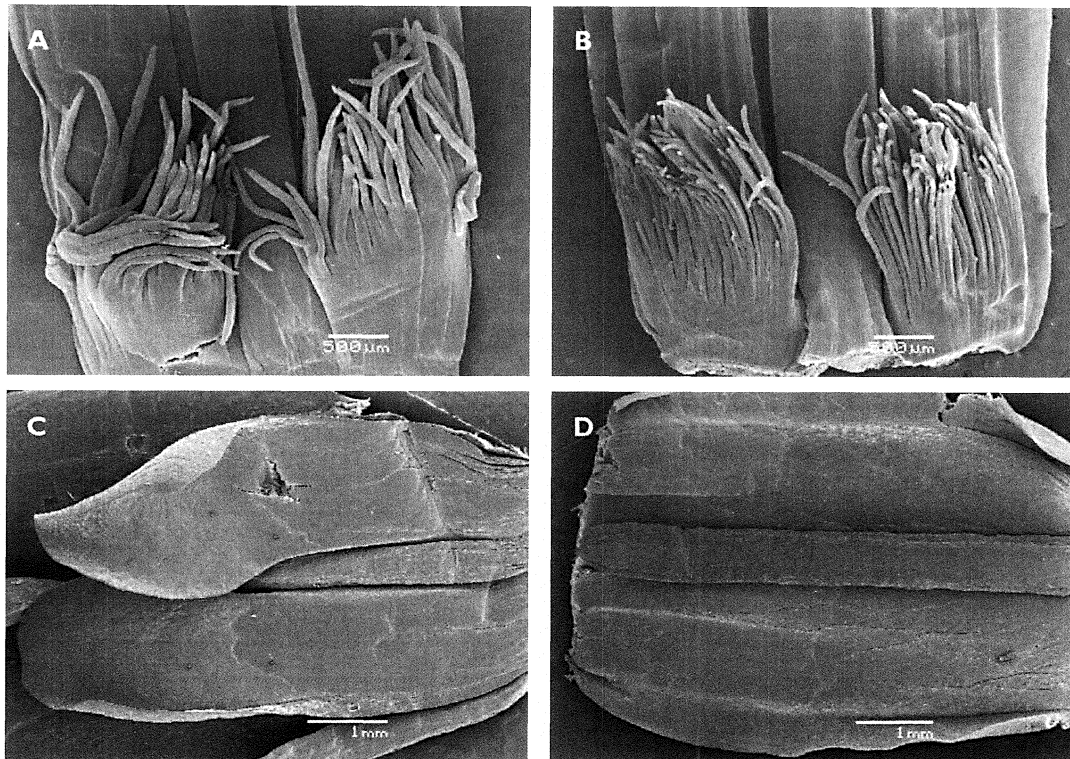


FIGURE 3. Petal appendages A. *Aechmea fasciata*. B. *A. chantinii*. C. *Vriesea vr* × *carinata*. D. *V. splendens*.

by hybrid sterility. F_1 -sterility in interspecific crosses is very common and may be the end result of reduced chromosome pairing during meiosis (Van Tuyl & De Jeu 1997). *Tillandsia cyanea* pollen was monosulcate (FIGURE 4F) of the “operculum” type (\pm compact, often centrally located exine elements on top of the sulcus, Halbritter 1992). Pollen grains were relatively small ($<100\ \mu\text{m}$). *Guzmania lingulata* and *A. chantinii* had inaperturate pollen. Inaperturate pollen was reported in three genera of Bromeliaceae: *Aechmea*, *Canistrum*, and *Guzmania* (Ehler & Schill 1973, Halbritter 1992). In inaperturate pollen, no defined germination pore is present and an opening is produced de novo by the pollen tube at germination. Only in a few families of aquatic plants, tropical monocots, and certain dicots is this pollen type present. In the inaperturate class, the exine may be fragile and much reduced. The intine is usually thick and prominent in these types (Knox 1984). Species with inaperturate pollen grains often originate from humid environments, and their pollen remain viable despite reduced and thin exines (Furness & Rudall 1999). *Aechmea chantinii* is widespread in the warm and humid lowland of

Amazonian South America (Luther 1997). *Guzmania lingulata*, however, occurs in a broader range of climates (70–1000 m elevation, from Guatemala to Colombia and northeastern Brazil) (Smith & Downs 1977). The exine of *Aechmea*, *Vriesea*, *Guzmania*, and *Tillandsia* species is mostly reticulate (a mesh-like pattern) (Erdtman & Praglowski 1974, Halbritter 1992), as in the studied cultivars except for *A. chantinii*.

The ovary is the basal region of the pistil that provides protection to the ovules (Knox et al. 1986). The ovary consisted of three carpels more or less fused at the edges. The ovules of the studied bromeliads were separated in three ovary chambers with a central placenta (FIGURE 5B, E). The ovules were attached on the placenta in several rows along the entire length of the ovary cavity of *Vriesea* (FIGURE 5C), *Guzmania*, and *Tillandsia* but only in the upper half for *Aechmea*. The ovules were anatropous (FIGURE 5D) and bitegmic with the micropyle formed by the inner integument. Ovules were densely packed on the placenta and characterised by a chalazal appendage (FIGURE 5A, F). A chalazal appendage produced from the funicle is present in many genera of Bromeliaceae (Gross 1988).

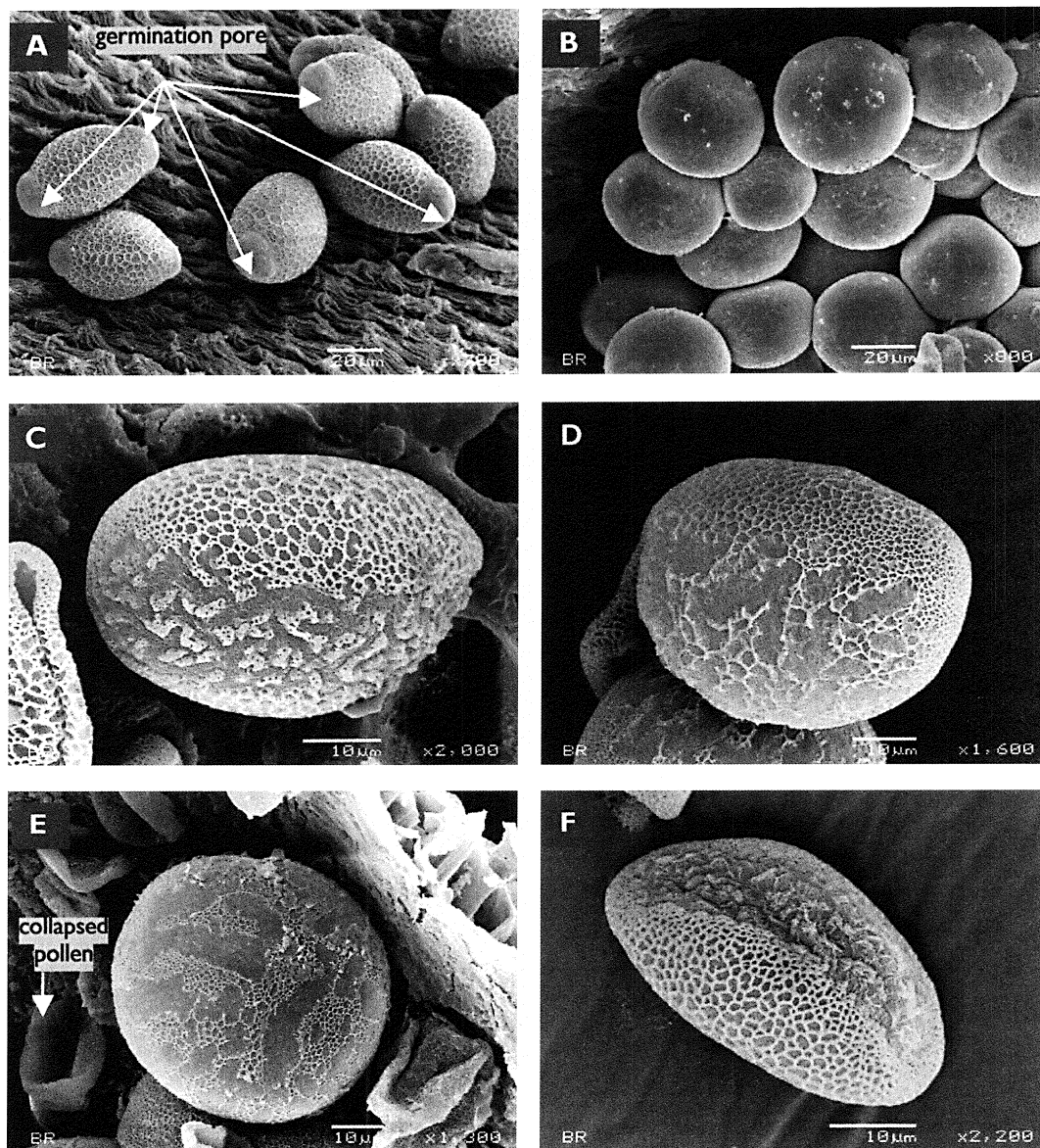


FIGURE 4. Pollen **A.** Pollen grains *Aechmea fasciata* ($\times 700$). **B.** Pollen grains of *A. chantinii* ($\times 800$). **C.** Pollen grain of *Vriesea vr \times carinata* ($\times 2000$). **D.** Pollen grains of *V. splendens* ($\times 1600$). **E.** Pollen grains of *Guzmania lingulata* ($\times 380$). **F.** Pollen grain of *Tillandsia cyanea* ($\times 2200$).

CONCLUSIONS

Important floral features for bromeliads are stigma type, petal appendages, and pollen and ovule appearance. Essential features for successful plant breeding are pollen viability and style length. The conduplicate-spiral stigma type was typical for *Aechmea*, which had ornately fringed petal appendages. Those of *Vrie-*

sea vr \times carinata were much larger and tongue-like blade. Petal appendages in *Vriesea splendens* were almost absent indicating the overemphasis of petal appendages in the circumscription of generic limits in Tillandsioideae (Brown & Terry 1992, Benzing 2000). Pollen grains of *V. vr \times carinata*, *V. splendens*, and *Tillandsia cyanea* were monosulcate. *Aechmea fasciata* possessed biporate pollen. Pollen

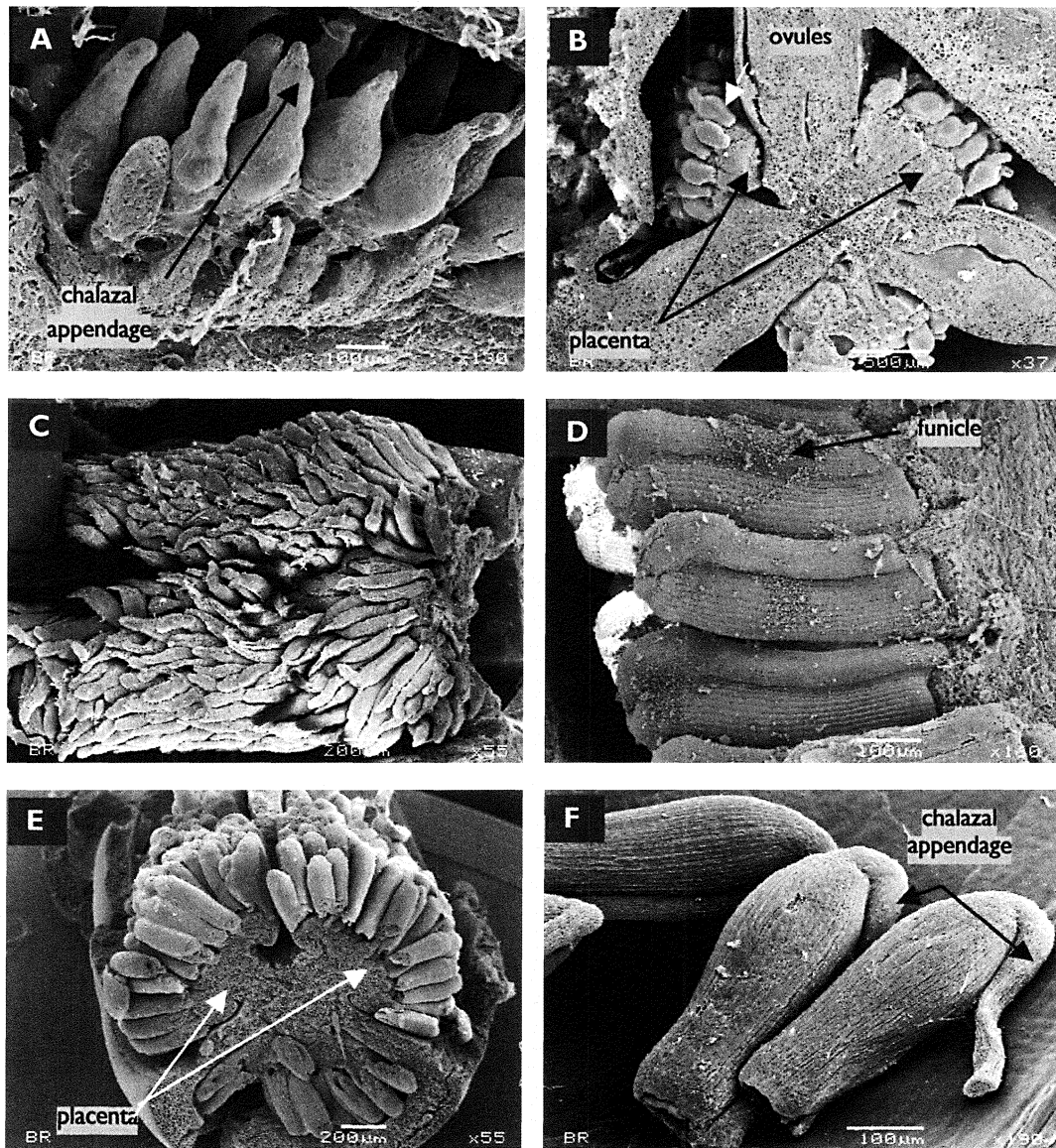


FIGURE 5. Ovary and ovules. **A.** Ovary and ovules of *Aechmea fasciata* ($\times 130$). **B.** Ovary and ovules of *A. chantinii* ($\times 37$). **C.** Ovules of *Vriesea* \times *viminalis rex* \times *carinata* ($\times 55$). **D.** Detail of ovules of *V. splendens* ($\times 160$). **E.** Ovary and ovules of *Guzmania lingulata* ($\times 55$). **F.** Detail of ovules of *Tillandsia cyanea* ($\times 190$).

of *A. chantinii* and *Guzmania lingulata* was of the unusual inaperturate class.

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